Fisheries and Oceans Canada | Pêches et Océans Canada
Ecosystems and Oceans Science | Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2015/044

Central and Arctic Region

Instantaneous availability bias correction for calculating aerial survey abundance estimates for narwhal (*Monodon monoceros*) in the Canadian High Arctic

Cortney A. Watt[1, 2], Marianne Marcoux[2], Natalie C. Asselin[3], Jack R. Orr[2], and Steven H. Ferguson[2]

[1]Department of Biological Sciences,
University of Manitoba,
Winnipeg, MB, Canada, R3T 2N2

[2]Fisheries and Oceans Canada,
501 University Crescent,
Winnipeg, MB, Canada, R3T 2N6

[3]Center for Earth Observation Science,
University of Manitoba,
Winnipeg, MB, Canada, R3T 2N2

July 2015

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

© Her Majesty the Queen in Right of Canada, 2015
ISSN 1919-5044

Correct citation for this publication:

Watt, C.A., Marcoux, M., Asselin, N.C., Orr, J.R., and Ferguson, S.H. 2015. Instantaneous availability bias correction for calculating aerial survey abundance estimates for narwhal (*Monodon monoceros*) in the Canadian High Arctic. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/044. v + 13 p.

TABLE OF CONTENTS

ABSTRACT iv
RÉSUMÉ v
INTRODUCTION 1
METHODS 2
  INSTRUMENTING THE ANIMALS 2
  DATA ANALYSIS 2
RESULTS 4
DISCUSSION 4
  2013 SURVEY 4
  FUTURE SURVEYS 5
RECOMMENDATIONS FOR 2013 SURVEY 6
RECOMMENDATIONS FOR FUTURE SURVEYS 6
ACKNOWLEDGEMENTS 6
LITERATURE CITED 7
TABLES 9
FIGURES 12

ABSTRACT

Twenty-four narwhals were fitted with satellite tags near the communities of Arctic Bay and Pond Inlet, Nunavut every August from 2009-2012 and provided information on the time narwhals spend at different depths. Aerial surveys to estimate narwhal abundance were also conducted in August 2013. An accurate estimate of narwhal abundance is needed for advising on a total allowable catch; however, not all narwhals are available for viewing during the survey as most may be submerged and therefore invisible to observers. Narwhals diving to greater than 2 m depths are not distinguishable from an aircraft in clear waters, while narwhals in highly turbid waters, such as that found in fiords where glacial runoff enters, may not be distinguishable at >1 m depths. A correction factor for this availability bias is needed to adjust survey estimates to account for narwhals that may have been present but were either not visible to observers, or not distinguishable from beluga whales. An instantaneous availability correction factor used to correct aerial surveys can be estimated from the proportion of time diving animals spend near the surface where they can be detected and identified. The proportion of time narwhals spent at 0-1 m, and 0-2 m depths was analyzed in a mixed effect model with whale as a random variable and period of August (mid versus late), time of day (day or night), sex, and area of tagging as fixed factors. The chosen model included no variables for the 0-1 m bin and period of August for the 0-2 m bin. Tagged narwhals spent 20.4 ± 0.78 % of their time in the 0-1 m bin in August and we recommend an instantaneous availability correction of 4.90 (± 0.187) for the 2013 survey in regions with highly turbid waters where visibility may be limited. Narwhals spent 31.4 ± 1.06 % of their time in the 0-2 m bin in mid August and we recommend an instantaneous correction of 3.18 (± 0.107) for 2013 survey strata occurring in clear waters.

Correction instantanée du biais de disponibilité pour le calcul des estimations de l'abondance des narvals (*Monodom monoceros*) tirées de relevés aériens dans l'Extrême-Arctique canadien

RÉSUMÉ

Vingt-quatre narvals ont été équipés d'émetteurs satellites près des collectivités d'Arctic Bay et de Pond Inlet, au Nunavut, tous les ans, en août, entre 2009 et 2012, ce qui nous a fourni des renseignements sur le temps passé par les narvals à différentes profondeurs. Des relevés aériens ont également été réalisés en août 2013 afin d'estimer l'abondance des narvals. Nous avons besoin d'une estimation fiable de l'abondance des narvals pour pouvoir déterminer le total autorisé des captures. Cependant, il est impossible de voir l'ensemble des narvals au cours du relevé étant donné que la plupart sont probablement immergés et, par conséquent, invisibles pour les observateurs. Depuis un avion, on ne peut distinguer les narvals qui plongent à des profondeurs de plus de 2 m dans des eaux claires. Dans les eaux fortement turbides, comme celles des fjords où pénètre le ruissellement des glaciers, on ne peut distinguer les narvals à des profondeurs supérieures à 1 m. Un facteur de correction de ce biais de disponibilité est nécessaire afin d'ajuster les estimations du relevé de manière à tenir compte des narvals qui étaient peut-être présents, mais que les observateurs ne pouvaient pas voir ou différencier des bélugas. Un facteur de correction instantanée de la disponibilité utilisé pour corriger les relevés aériens peut être estimé à partir de la proportion de temps que les animaux en plongée passent près de la surface de l'eau, où ils peuvent être détectés et identifiés. Le temps passé par les narvals à des profondeurs de 0-1 m et de 0-2 m a été analysé dans un modèle à effets aléatoires, où la baleine était la variable aléatoire et la période en août (la mi-août par rapport à la fin août), le moment de la journée (jour ou nuit), le sexe et la zone d'étiquetage étaient les facteurs fixes. Le modèle choisi ne comprenait aucune variable pour les profondeurs de 0-1 m et la période d'août pour les profondeurs de 0-2 m. Les narvals étiquetés ont passé 20,4 ± 0,78 % de leur temps dans les profondeurs de 0-1 m en août, et nous recommandons une correction instantanée de la disponibilité de 4,90 (± 0,187) pour les relevés de 2013 dans les régions où les eaux sont fortement turbides et où la visibilité est donc limitée. Les narvals ont passé 31,4 ± 1,06 % de leur temps dans les profondeurs de 0-2 m à la mi-août, et nous recommandons une correction instantanée de 3,18 (± 0,107) pour la strate de relevé de 2013 qui a eu lieu dans des eaux claires.

INTRODUCTION

Narwhals (*Monodon monoceros*) are part of the annual hunt in Greenland and the Canadian Arctic. Narwhals in Baffin Bay, known as the Baffin Bay population, are one of only three narwhal populations in the world (Petersen et al. 2011). This population is known to be the largest, with estimates of abundance suggesting more than 60,000 individuals (Richard et al. 2010). Although this population is quite large, communities all along the west coast of Greenland and northern Canada hunt narwhals at all times of year, and therefore the population is a shared resource among the communities. Narwhals in this population overwinter in the Davis Strait, sometimes entering Disko Bay and becoming available to hunters (Watt et al. 2012), and spend summer in fiords and inlets in western Greenland and northern Canada. Narwhals seem to display fidelity to specific summering grounds, using the same regions year after year. As a result, managers have subdivided the population into what are referred to as management stocks. To estimate the abundance of each of these stocks and to update the previous population abundance estimate, aerial surveys were conducted in August 2013.

To determine a sustainable harvest level, and make recommendations for total allowable catches, an estimate of the total narwhal abundance is necessary. Population estimates are often determined using aerial surveys, with cameras and multiple observers on each side of the plane. Although this method can cover a large area and capture a large proportion of the population, many whales may be diving deeper than can be seen from the air. A study by Richard et al. (1994) found that models of narwhal of similar morphological proportions could not be identified to species during aerial surveys, irrespective of the altitude flown (360 m, 370 m, 680 m, or 990 m), if they were submerged deeper than approximately two meters. To accurately estimate the abundance of narwhals, a correction for the proportion of time that narwhals are available (i.e. visible and distinguishable from beluga whales) to observers is required. An instantaneous availability correction factor can be used to correct photographic aerial survey and is an important component of the availability correction factor used for visual aerial surveys. This correction can be estimated from the proportion of time diving animals spent near the surface where they can be detected and identified. Previous research has evaluated the time narwhals spent in different depth bins and found that narwhals from Baffin Bay spent variable amounts of time at or near the surface. For instance, Martin et al. (1994) estimated narwhals spent ~51% of their time at 0 – 3 m depths, Heide-Jørgensen et al. (2001) found narwhals spent 22 % of their time at 0-1 m depths, Innes et al. (2002) estimated they spent 38 % of their time at 0-2 m depths, and Laidre et al. (2002) found they spent between 30-53 % of their time at depths < 5 m. As dive behavior can vary based on location and season, an updated estimate of narwhal availability, specific to the region and time of the aerial surveys, was needed. We have two main objectives in this study. The first, and most important, is to provide corrections for the 2013 narwhal survey by evaluating factors that may impact availability bias estimates. Secondarily, we wanted to evaluate behaviour of narwhals at the surface and provide information relevant to providing correction information to past and future surveys. We evaluated the time narwhals spent in both the 0-1 m and 0-2 m bins. Narwhals can be viewed from aircraft up to 2 meters in clear water (Richard et al. 1994); however, aerial surveyors in 2013 noted that the water was murky in some specific surveyed regions as a result of increased silt in the water. Due to this, we chose to also calculate the time spent in the 0-1 m bin, providing an estimate that could be used in regions where surveyors decide that narwhals may not be seen up to 2 m depth.

METHODS

INSTRUMENTING THE ANIMALS

Satellite linked time depth recorder tags (SPLASH tags, Wildlife Computers) were deployed on narwhals to transmit daily information on their location and diving behaviour. Seven narwhals, three females and four males, were tagged at Kakiak Point (72° 41' 00" N, 86° 41' 20" W) in Admiralty Inlet, near the community of Arctic Bay, Nunavut, in August 2009 (Fig. 1, Table 1). In Tremblay Sound (72° 21' 23" N, 81° 6' 24" W), near the community of Pond Inlet, Nunavut in August 2010-2012, seventeen narwhals were tagged, twelve females and five males (Fig. 1, Table 1). Methods for narwhal capture have previously been published (Dietz et al. 2001, Orr et al. 2001, Heide-Jørgensen et al. 2003, Dietz et al. 2008). In short, narwhals were captured in nets set perpendicular to the shore. Once caught, two inflatable zodiac boats with three passengers each would boat out to the net, pull the whale to the surface, and bring them closer to shore for instrumentation with a satellite-linked transmitter. Narwhals were held in shallow water by fitting a hoop net over their head (for females) or holding the tusk (for males). A rubberized tail rope was used to stabilize the animal. Two to three 10 mm nylon pins were then placed through the dorsal ridge and the tag was anchored to the pins. The process was approved by the Freshwater Institute Animal Care Committee (FWI-ACC-2009-024, FWI-ACC-2010-001, FWI-ACC-2011-016, FWI-ACC-2012-009) and veterinarians monitored narwhals throughout.

DATA ANALYSIS

Location data was obtained from the ARGOS system (CLS America). Data was transmitted every two hours but was summarized into four 6-hour histograms, referred to from their starting time, *i.e.* 3:00, 9:00, 15:00 and 21:00 local time at deployment location, every day throughout the month of August with a single location (longitude and latitude) reported for each 6-hour time block, which is the most accurate location estimate collected in the previous 24-hours. For each 6-hour period, all tags provided the time the narwhal spent at different depths, combined in bins. All tags were programmed with the same depth bins to calculate the proportion of time narwhals spent in the 0-1 m and 0-2 m depth bins with a resolution of 0.5 m (Wildlife Computers). Although narwhal models were not identifiable to species when submerged deeper than two meters, they may be even harder to see when congregating in fiords with silty water. Therefore, an availability bias was also calculated for the 0-1 m bin in order to provide a different correction for narwhals in turbid water. Diving behaviour 24-hours post tagging was ignored for analysis after visual inspection of the data because the whale's behaviour may have been altered as a result of the tagging process (Geertsen et al. 2004, Norman et al. 2004, Elwen et al. 2006).

Models with whale as a random variable and area, sex, time of day, and period of August as fixed effects, were fitted to predict the proportion of time narwhals spent in the 0-1 and 0-2 m depth bins. The dependent variable of the models was the proportion of time spent in each different depth bin. Transmissions from the periods starting at 9:00 and 15:00 were considered daytime, while those from the periods starting at 21:00 and 3:00 were considered night. Period of August was also incorporated because narwhals tend to make more extensive movements later in August (Dietz et al. 2001, Heide-Jørgensen et al. 2002, Heide-Jørgensen et al. 2003, Dietz et al. 2008, Watt et al. 2012), and dive behaviour may change during this phase of movement. The final week of August (August 25-31) was identified as "late August," based on previous tracking studies showing this is a period of greater narwhal movements, while

August 13 (the earliest tagging date) until August 24 was labeled as "mid August". These sub-divisions were chosen prior to determining the survey results since we wanted to make a division based on narwhal movements that could be used for the 2013 and future surveys. Individual percentage of time in 0-1 m and 0-2 m bins was estimated as an average of all the 6-hour bins collected for that whale (Table 1; n is reported for each whale).

We modeled the percentage of time narwhals spent in each depth bin with a linear mixed-effect model of log-transformed data (logged percentage of time; Fig. 2, Table 2). This approach has been suggested for log-normal data (Zuur et al. 2010, Borcard et al 2011, Sokal and Rohlf 2012). Then, we used a backwards-step-wise approach to evaluate the fixed-effect to include in the model for each of the depth bins. The selection started with the full model (with fixed effects period of August, time of day, sex, and area). The significance of each fixed effect was evaluated by comparing the fit of the models with and without the term of interest using maximum likelihood ratio tests ($\chi 2$ distribution, df = the difference in the degrees of freedom between the nested models). The least significant fixed effect was dropped and the process was repeated until no effect could be further removed ($p < 0.05$). Statistical analyses were performed using the packages gamlss (Rigby and Stasinopoulos 2005) and lme4 (Bates et al. 2014) in the statistical software R (R Development Core Team 2010).

To provide more general information on narwhal dive behavior that may be relevant to future investigations, we also considered environmental variables that likely impact the time narwhals spent at or near the surface. Variables of interest that may impact dive depths and time spent near the surface included presence of ice, depth (m), distance from shore (km), and bathymetric slope. Although sea ice is considered to have an important effect on narwhal behaviour (Laidre et al. 2003), we were unable to evaluate its impacts due to a lack of sea ice in the locations used by the tagged narwhals in August 2009-2012. Bathymetric 500 x 500 m tiff grid files were downloaded from the International Bathymetric Chart of the Arctic Ocean (IBCAO) and imported into ArcGIS in order to extract depth for each narwhal position (a single location was provided for each 6-hour time block based on the best available location for the previous 24 hours (Jakobsson et al. 2012). Slope and distance to land were extracted using the spatial analysis tools within ArcGIS. In some cases, particularly in narrow fiords and inlets, narwhal locations appeared on land as a result of the error associated with the location data points. In these instances, depth extractions were positive and inaccurate and the previous in-water depth measure was used. The previous in-water depth measure may have been up to two previous recordings or 12 hours earlier. Distance from shore and depth were significantly correlated ($r = 0.77$, $p < 0.0001$) and therefore only depth and slope were considered in further analysis. We evaluated the effect of environmental factors on the time narwhals spent at depth using the same backwards-step-wise approach described above.

Lastly, we considered significant effects from the statistical models and calculated weighted averages to determine the average time all whales spent in the 0-1 m and 0-2 m bins. Weighted averages took the average for each whale, weighted it based on the number of 6-hour blocks collected, and calculated an overall average. Standard errors were calculated using a weighted standard deviation divided by the square-root of the number of narwhals used in each calculation.

RESULTS

The best linear mixed-effects model for the 0-1 m depth bin did not include any fixed effect while the 0-2 m depth bins included period of August (Table 3).

Using a weighted average and standard error, narwhals (n = 24) spent 20.4 ± 0.78 % of their time in the 0-1 m bin in August. In August, individual narwhals spent between 12.3 ± 0.54 % and 29.3 ± 0.79 % of their time within 0-1 m of the surface (Table 1). A male tagged in Admiralty Inlet spent the least amount of time and a female tagged in Tremblay Sound spent the most time in the 0-1 m bin (Table 1).

In the 0-2 m bin, narwhals (n = 23) spent 31.4 ± 1.06 % in mid August with individual narwhals ranging from 25.4 ± 1.34 % to 41.4 ± 4.87 %. Both extremes came from female narwhals tagged in Tremblay Sound (Table 1). In late August narwhals (n = 24) spent an average of 31.6 ± 0.86 % of their time in the 0-2 m bin.

The environmental factor slope did not improve the fit of the models while the factor depth improved the fit of the models for both the 0-1 and 0-2 m depth bins (Table 3). Narwhals spent more time within 1 or 2 m of the surface in deeper water than in shallower water (Fig. 3).

DISCUSSION

Here, we calculated the availability bias from Baffin Bay narwhals tagged in 2009-2012 that is an update to bias estimates calculated for narwhals in 1993-1999 (Martin et al. 1994, Heide-Jørgensen et al. 2001, Innes et al. 2002, Laidre et al. 2002). In August we found narwhals spent 20.4 % of their time in the 0-1 m bin, which is slightly less than the 22 % found by Heide-Jørgensen et al. (2001). We found narwhals spent 31.4 % of their time in the 0-2 m bin in mid-August, which is very similar to Northern Hudson Bay narwhals who were found to spend 31.6 % of their time in the 0-2 m bin (Westdal et al. 2013). The two whales that spent the most time in the 0-1 m and 0-2 m bins in August were female narwhals from Tremblay Sound. Both of these females were captured with calves and thus were less likely to spend time at depth as they would be limited by the diving ability of their calves. Individual differences highlight the need to have telemetry information from proportionally similar life history stages as found in the wild population.

2013 SURVEY

There was a significant effect of period of August for the 0-2 m bin; however, the majority of the 2013 narwhal survey occurred in mid August with only 10 sightings occurring after that, all on August 25, and thus we recommend availability bias corrections based on mid August for analysis of the 2013 survey data.

Although we did consider environmental variables, and depth was a significant factor, it is important to acknowledge that these depth extractions are only best estimates and for this reason we chose to use the model that excludes depth for the 2013 survey. The bottom bathymetry of this region has not been mapped in detail. We used IBCAO to assign a bottom bathymetry to each narwhal location. Bathymetries are largely based on ship tracking sounds with interpolation between soundings, and in the Arctic shipping traffic has been limited and thus many data points are interpolated (Jakobsson et al. 2012). For instance, a single depth is extracted within a 500 m^2 grid, which means at some points, the nearest depth interpolated estimate can be up to 354 m away and the actual depth sounding measurements even further.

This is not ideal, but is currently the best bathymetric information for this region, and although it is important to consider these environmental variables when evaluating availability bias, it is also important to understand the limitations of the currently available data. Similarly, for the surveyors to use this information, they would also need to know the depth the sighted narwhals were at when surveyed, and would have a similar issue attempting to assign depths (i.e., large uncertainty). Because of the unknown bias this could incorporate into the abundance estimates, we suggest corrections for the 2013 survey estimates use the general model that excludes depth.

The depth bins programmed for time spent at depth have an error associated with them of 0.5 m (Wildlife Computers). Essentially this means the depth at which a narwhal is at has an error of 0.5 m associated with it, and if a whale is at 1.4 m, the time that whale is at that depth would fall in the 1-2 m bin, but could fall into either 0-1 m or 1-2 m bins once the error is incorporated. We did not incorporate this error into the variance for the time spent at depth in the 0-1 or 0-2 m bins for corrections for the 2013 survey and it is important to recognize that we may be under-estimating the variance by not factoring in this error.

FUTURE SURVEYS

Future surveys should take into consideration the fact that narwhals seem to have different time-at-surface behaviour in the latter part of August, related to increases in directional movement as they prepare for migration to the wintering area (Watt et al. 2012). The period of August is a factor that should be considered both when planning future surveys, and also when analyzing the data after the survey is complete as the dates when movements begin to increase may change with changes in climate and open-water availability (e.g., Northern Hudson Bay population; (Watt and Ferguson 2014)).

Future surveys may also want to consider depth as an important environmental covariate in future estimates, since we did find that depth (even though it was only very roughly estimated in this study) has an impact on the time narwhals spend at the surface. More specifically, it appears that narwhals may spend more time at the surface when they are in shallow waters compared to deep regions and this may be useful information for correcting surveys in the future, when, we assume, the bathymetric profiles of these regions will be mapped in much better detail.

Future analyses may want to consider factoring in the error associated with the programmed tags (i.e., 0.5 m) as this may be an important source of uncertainty in calculating abundance estimates. Although it would not change the average percent of time spent in the different depth bins, it would increase the error associated with the bins and subsequently the error associated with the correction factors.

We were unable to consider sea ice presence or absence in this study, but it may be an important factor and should be considered in survey years and regions when ice is present. Similarly, future surveys may have to account for the presence of predators, such as killer whales (*Orcinus orca*), which have increased in the Canadian Arctic since 1850 (Higdon and Ferguson 2009, Higdon et al. 2012), and may have an impact on narwhal behaviour (Laidre et al. 2006) and the time they spend in the 0-1 m and 0-2 m bins.

RECOMMENDATIONS FOR 2013 SURVEY

For population estimates of Baffin Bay narwhals using aerial surveys conducted in mid August, in regions with clear water we recommend incorporating an instantaneous availability correction factor based on the 0-2 m depth bin of 3.18 (± 0.107) since narwhals spent 31.4 ± 1.06 % of their time in the this depth bin. In fiords and other regions with murky waters that limit the ability of aerial observations of narwhal, we recommend using a correction based on the 0-1 m depth bin. Narwhals spent 20.4 ± 0.78 % of their time in the 0-1 m bin and thus we recommend using an instantaneous availability correction factor of 4.90 (± 0.187). We recommend using these corrections for all narwhals surveyed from the Baffin Bay population, even though it is based on telemetry data collected from two stocks (the Eclipse Sound and Admiralty Inlet stocks). We assume that since there was no significant difference in the time spent in different depth bins for narwhals from these two stocks that other narwhal stocks of the Baffin Bay population are also behaving in a similar fashion.

RECOMMENDATIONS FOR FUTURE SURVEYS

We recommend future surveys and analyses on time spent by narwhals at the surface may benefit from

1) incorporating depth as an environmental covariate in their models,
2) evaluating whether their results apply to all narwhal stocks being surveyed by considering the summer aggregation area as a factor in their model,
3) timing their survey to occur only in early and mid August as previous telemetry data has shown that narwhal begin making more extensive movements in later August resulting in mixing of narwhals from different summer aggregation areas (Watt et al. 2012), and
4) considering using other models such as beta regressions, because they are designed for data restricted between zero and one (Ferrari and Cribari-Neto 2004, Figueroa- Zúniga et al 2013), or generalized linear mixed-effect models with link functions.

ACKNOWLEDGEMENTS

All work was conducted under DFO License to Fish, and prior approval was obtained from the Freshwater Institute Animal Care Committee. We would like to thank the many dedicated people in the research field camps for their valuable assistance with the handling and instrumenting of the narwhals, particularly S. Black who offered veterinarian assistance. We thank the Hunters and Trappers Organizations in Arctic Bay and Pond Inlet, Nunavut, Canada, for all of their support. We also thank the Polar Continental Shelf Program for logistic support, and Fisheries and Oceans Canada, the Nunavut Wildlife Management Board, Nunavut Implementation Fund, World Wildlife Fund Canada, and ArcticNet for funding. NSERC, the Northern Scientific Training Program, the E. Scherer Memorial scholarship, and the Garfield Weston Foundation provided personal funding to CAW.

LITERATURE CITED

Bates, B., Maechler, M., Bolker,B., and Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Borcard D., Gillet, F., and Legendre, P. 2011. Numerical Ecology with R. Springer, New York.

Dietz, R., Heide-Jørgensen, M.P., Richard, P., Orr, J., Laidre, K., and Schmidt, H.C. 2008. Movements of narwhals (*Monodon monoceros*) from Admiralty Inlet monitored by satellite telemetry. Polar Biol. 31: 1295–1306.

Dietz, R., Heide-Jørgensen, M.P., Richard, P.R., and Acquarone, M. 2001. Summer and fall movements of narwhals (*Monodon monoceros*) from northeastern Baffin Island towards northern Davis Strait. Arctic 54: 244–261.

Elwen, S., Meyer, M.A., Best, P.B., Kotze, P.G.H., Thornton, M., and Swanson, S. 2006. Range and movements of female heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-linked telemetry. J. Mammal. 87: 866–877.

Ferrari, S. and Cribari-Neto, F. 2004. Beta regression for modelling rates and proportions. J. Appl. Stat. 31: 799–815.

Figueroa-Zúniga, J.I., Arellano-Valle, R.B., and Ferrari, S.L. 2013. Mixed beta regression: A Bayesian perspective. Comput. Stat. Data Anal. 61: 137–147.

Geertsen, B.M., Teilmann, J., Kastelein, R.A., Vlemmix, H.N.J., and Miller, L.A. 2004. Behaviour and physiological effects of transmitter attachments on a captive harbour porpoise (*Phocoena phocoena*). J. Cetacean Res. Manag. 6: 139–146.

Heide-Jørgensen, M.P., Dietz, R., Laidre, K., and Richard, P. 2002. Autumn movements, home ranges, and winter density of narwhals (*Monodon monoceros*) tagged in Tremblay Sound, Baffin Island. Polar Biol. 25: 331–341.

Heide-Jørgensen, M.P., Dietz, R., Laidre, K.L., Richard, P., Orr, J., and Schmidt, H.C. 2003. The migratory behaviour of narwhals (*Monodon monoceros*). Can. J. Zool. 81: 1298–1305.

Heide-Jørgensen, M.P., Hammeken, N., Dietz, R., Orr, J., and Richard, P.R. 2001. Surfacing times and dive rates for narwhals (*Monodon monoceros*) and belugas (*Delphinapterus leucas*). Arctic 54: 284–298.

Higdon, J.W. and Ferguson, S.H. 2009. Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. Ecol. Appl. 19: 1365–1375.

Higdon, J.W., Hauser, D.D.W., and Ferguson, S.H. 2012. Killer whales (*Orcinus orca*) in the Canadian Arctic: Distribution, prey items, group sizes, and seasonality. Mar. Mamm. Sci. 28: E93–E109.

Innes, S., Heide-Jørgensen, M.P., Laake, J.L., Laidre, K.L., Cleator, H.J., Richard, P., and Stewart, R.E.A. 2002. Surveys of belugas and narwhals in the Canadian High Arctic in 1996. NAMMCO Sci. Publ. 4: 169–190.

Jakobsson, M., Mayer, L., Coakley, B., et al. 2012. The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0, Geophys. Res. Lett. Geophysical Research Letters 39:DOI: 10.1029/2012GL052219.

Laidre, K.L., Heide-Jørgensen, M.P., and Dietz, R. 2002. Diving behaviour of narwhals (*Monodon monoceros*) at two coastal localities in the Canadian High Arctic. Can. J. Zool. 80: 624–635.

Laidre, K.L., Heide-Jørgensen, M.P., Dietz, R., Hobbs, R.C., and Jørgensen, O.A. 2003. Deep-diving by narwhals *Monodon monoceros*: differences in foraging behavior between wintering areas? Mar. Ecol. Prog. Ser. 261: 269–281.

Laidre, K.L., Heide-Jørgensen, M.P., and Orr, J.R. 2006. Reactions of narwhals, *Monodon monoceros*, to killer whale, *Orcinus orca*, attacks in the eastern Canadian Arctic. Can. Field-Nat. 120: 457–465.

Martin, A.R., Kingsley, M.C.S., and Ramsay, M.A. 1994. Diving behaviour of narwhals (*Monodon monoceros*) on their summer grounds. Can. J. Zool. 72: 118–125.

Norman, S.A., Hobbs, R.C., Foster, J., Schroeder, J.P. and Townsend, F.I. 2004. A review of animal and human health concerns during capture-release, handling and tagging of odontocetes. J. Cetacean Res. Manag. 6: 53–62.

Orr, J.R., Joe, R., and Evic, D. 2001. Capturing and handling of white whales (*Delphinapterus leucas*) in the Canadian Arctic for instrumentation and release. Arctic 54: 299–304.

Petersen, S.D., Tenkula, D., and Ferguson, S.H. 2011. Population genetic structure of narwhal (*Monodon monoceros*). DFO Can. Sci. Advis. Sec. Res. Doc. 2011/021. vi + 20 p.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Richard, P., Weaver, P., Dueck, L., and Barber, D.G. 1994. Distribution and numbers of Canadian High Arctic narwhals (*Monodon monoceros*) in August 1984. Meddelelser om Grønland, Bioscience 39: 41–50.

Richard, P.R., Laake, J.L., Hobbs, R.C., Heide-Jørgensen, M.P., Asselin, N.C., and Cleator, H. 2010. Baffin Bay narwhal population distribution and numbers: aerial surveys in the Canadian high Arctic, 2002–04. Arctic 63: 85–99.

Rigby, R.A., and Stasinopoulos, D.M. 2005. Generalized additive models for location, scale and shape. J. Appl. Stat. 54: 507–554.

Sokal R.R., and Rohlf, F.J. 2012. Biometry. Fourth Edition. MacMillan Publishing Company, New York.

Watt, C.A., and Ferguson, S.H. 2014. Fatty acids and stable isotopes (δ13C and δ15N) reveal temporal changes in narwhal (*Monodon monoceros*) diet linked to migration patterns. Mar. Mamm. Sci. 31:21-44. doi: 10.1111/mms.12131.

Watt, C.A., Orr, J., LeBlanc, B., Richard, P., and Ferguson, S.H. 2012. Satellite tracking of narwhals (*Monodon monoceros*) from Admiralty Inlet (2009) and Eclipse Sound (2010-2011). DFO Can. Sci. Advis. Sec. Res. Doc. 2012/046. iii + 17 p.

Westdal, K.H., Richard, P.R., and Orr, J.R. 2013. Availability bias in population survey of Northern Hudson Bay narwhal (*Monodon monoceros*). Polar Biol. 36: 1235–1241.

Zuur, A.F., Leno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1: 3–14.

TABLES

Table 1. Deployment date, sex, morphometric data, and the average percent of time spent in the 0-1 m and 0-2 m bins (± SE) for narwhals tagged with satellite-linked transmitters. The number of 6-hour blocks used to calculate the averages for the 0-1 and 0-2 m bins are also presented.

Tagging Area	Deployment Date	Sex	Tag Number	Length (m)	Fluke Length (m)	Tusk length (m)	n - number of 6-hour blocks (0-1 m, 0-2 m)	Average % time at 0-1 m ± SE in August	Average % time at 0-2 m ± SE in mid-August
Admiralty Inlet	2009-08-15	F	39290	3.74	0.86	-	62, 34	24.0 ± 0.87	35.0 ± 1.22
Admiralty Inlet	2009-08-15	M	39309	3.77	0.86	0.79	57, 30	19.0 ± 0.87	34.0 ± 2.35
Admiralty Inlet	2009-08-16	F	39313	3.91	0.89	-	58, 30	16.1 ± 0.48	31.2 ± 2.56
Admiralty Inlet	2009-08-17	M	39311	3.07	0.76	0.51	50, 24	12.3 ± 0.54	36.4 ± 2.41
Admiralty Inlet	2009-08-17	M	39256	4.50	1.07	1.65	54, 26	23.7 ± 0.62	29.1 ± 1.30
Admiralty Inlet	2009-08-17	M	39287	4.39	1.04	1.50	54, 26	20.7 ± 1.13	30.9 ± 1.72
Admiralty Inlet	2009-08-18	F	39249	3.86	0.94	-	49, 21	16.0 ± 0.74	36.5 ± 2.26
Tremblay Sound	2010-08-21	M	51871	4.44	1.07	1.56	39, 11	20.0 ± 0.67	27.6 ± 2.35
Tremblay Sound	2010-08-21	M	51872	4.61	1.03	1.00	39, 11	19.4 ± 0.65	30.5 ± 1.74
Tremblay Sound	2010-08-22	F	51873	4.00	0.90	-	35, 7	20.5 ± 0.81	41.4 ± 4.87
Tremblay Sound	2010-08-22	F	51874	3.90	0.96	-	34, 6	19.8 ± 0.70	32.3 ± 3.08
Tremblay Sound	2010-08-24	F	51875	3.80	0.93	-	24, -	18.8 ± 1.03	-
Tremblay Sound	2011-08-16	F	51876	3.91	0.85	-	56, 29	21.0 ± 0.54	29.8 ± 1.74
Tremblay Sound	2011-08-16	M	51878	3.10	0.76	0.20	57, 29	20.4 ± 0.71	29.1 ± 1.04
Tremblay Sound	2011-08-16	F	51879	4.01	0.91	-	55, 27	13.8 ± 0.51	34.2 ± 1.51
Tremblay Sound	2011-08-18	F	39314	4.06	0.93	-	50, 23	18.4 ± 0.43	32.4 ± 2.02
Tremblay Sound	2011-08-18	F	39270	3.94	0.97	-	49, 22	23.2 ± 1.06	32.2 ± 1.60

Tagging Area	Deployment Date	Sex	Tag Number	Length (m)	Fluke Length (m)	Tusk length (m)	n - number of 6-hour blocks (0-1 m, 0-2 m)	Average % time at 0-1 m ± SE in August	Average % time at 0-2 m ± SE in mid-August
Tremblay Sound	2011-08-19	F	39315	3.89	0.95	-	45, 17	23.0 ± 0.76	33.9 ± 1.58
Tremblay Sound	2011-08-19	F	57590	4.04	1.04	-	46, 18	16.9 ± 0.82	30.6 ± 1.56
Tremblay Sound	2012-08-13	F	115956	3.96	0.91	-	67, 39	29.3 ± 0.79	29.4 ± 1.17
Tremblay Sound	2012-08-14	M	115957	3.48	0.86	0.66	65, 37	20.6 ± 0.65	29.6 ± 1.12
Tremblay Sound	2012-08-17	F	115958	3.90	0.91	-	54, 26	22.9 ± 0.61	29.6 ± 1.58
Tremblay Sound	2012-08-18	M	115959	4.40	1.10	1.25	51, 23	23.6 ± 1.05	28.0 ± 1.41
Tremblay Sound	2012-08-19	F	115960	2.62	0.58	-	44, 18	22.4 ± 0.59	25.4 ± 1.34

Table 2. Summary statistics of residual errors for the best linear mixed-effect model of log-transformed data for different depth bins. The Filliben correlation coefficient is the coefficient of the correlation between the normal theoretical quantiles and the quantiles of the residual errors.

Summary statistics	0-1 m	0-2 m
Mean	0	0
Variance	0.064	0.051
Skewness	0.065	0.249
Kurtosis	4.359	3.236
Filliben Correlation	0.994	0.997

Table 3. Best linear mixed-effect models to predict the log-transformed proportion of time narwhals spent in depth bins. Models were selected using a backwards-step-wise approach. P-values were calculated using maximum likelihood ratio tests between the model with and without the effect investigated. All models include the random effect of whale.

	Fixed effects	Estimate	Standard Error	Likelihood Ratio Test	df	P value
0-1 m	Intercept	-1.65	0.03863	-	-	-
0-1 m with environmental variables	Intercept	-1.7	0.04031	-	-	-
	Depth	0.000217	$3.51*10^{-5}$	37.7	1	<0.0001
0-2 m	Intercept	-1.18	0.02694	-	-	-
	Period of August - Mid	-0.0434	0.01359	10.11	1	0.0015
0-2 m with environmental variables	Intercept	-1.23	0.02833	-	-	-
	Period of August - Mid	-0.0234	0.01419	2.72	1	0.0992
	Depth	0.000148	$3.305*10^{-5}$	19.92	1	<0.0001

FIGURES

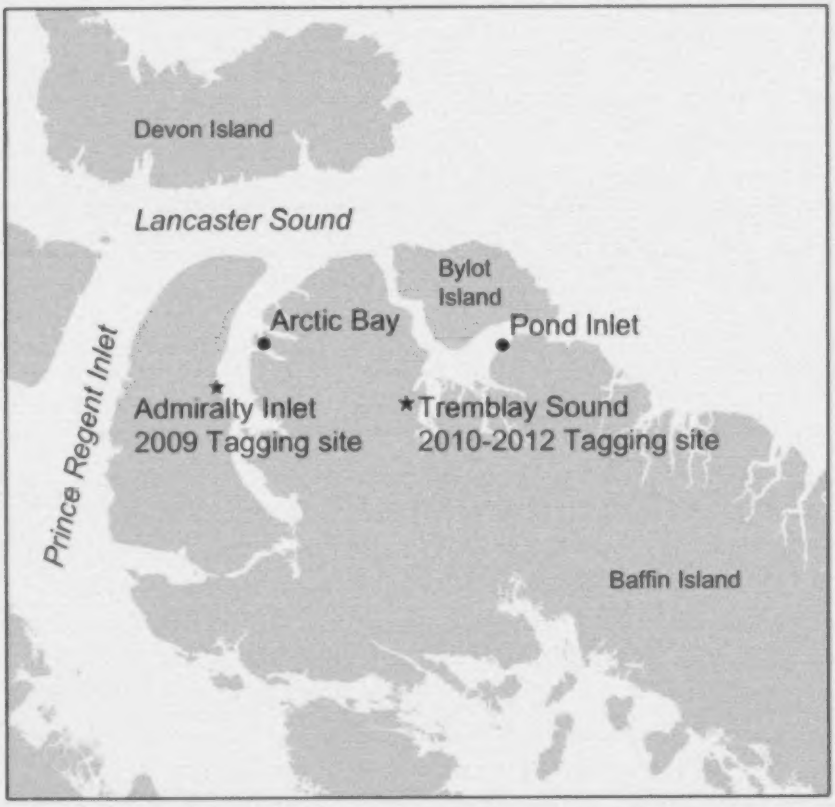

Figure 1. Map indicating the tagging areas (star) and closest communities in Canada where narwhals were fitted with satellite telemetry tags (circle).

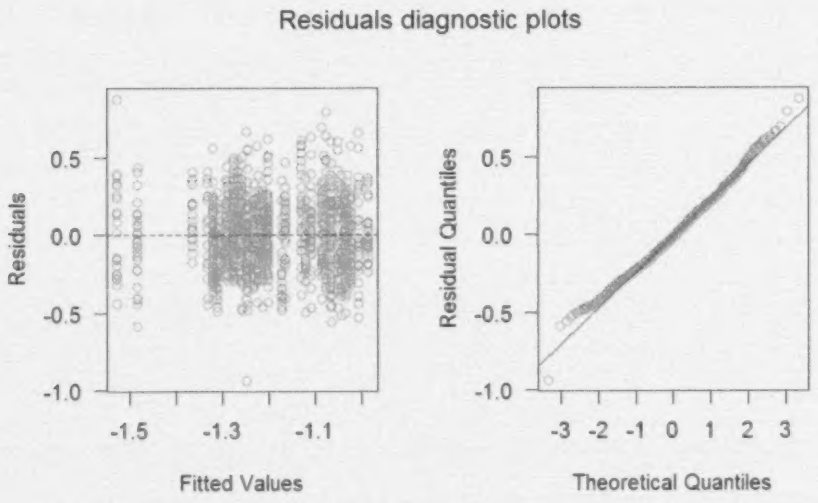

Figure 2. Example of residuals diagnostic plots for the best models to predict the logged proportion of time narwhals spent in 0-2 m depth bins (model selected: log(time at 0-2m)~ period of August + random (narwhal ID)).

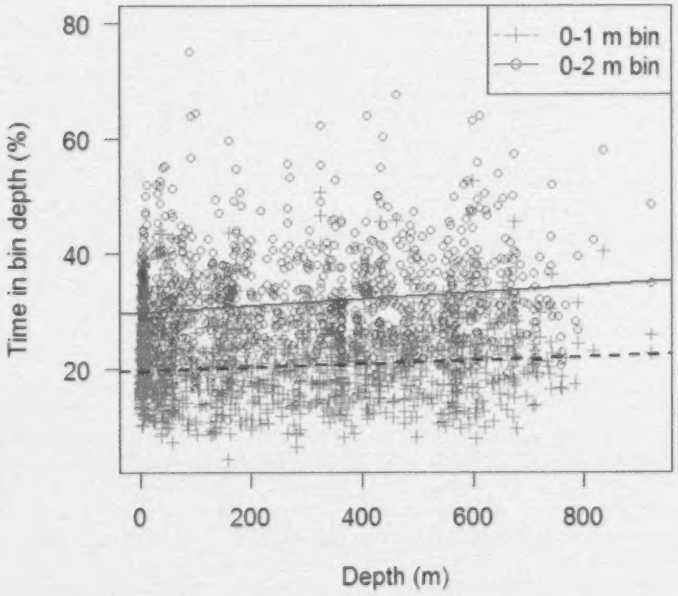

Figure 3. Relationship between water-column depth and percentage of time narwhals spent in 0-1 m and 0-2 m depth bins.